PREDATION AND SHELL DAMAGE IN A VISÉAN BRACHIOPOD FAUNA

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ABSTRACT. A description is given of a variety of borings and signs of predation which occurred either during the life or after the death of some Viséan brachiopods. These structures, thought to have been produced by sponges, bryozoans, gastropods, and fish are of interest as indicators of environment and of the type of death assemblage met within these rocks.

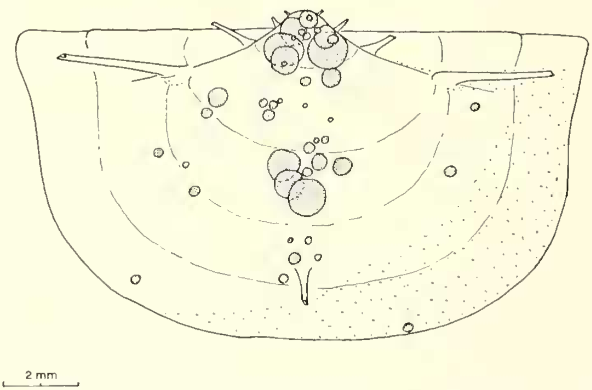
A RICH silicified brachiopod fauna obtained from Upper Viséan rocks in Co. Fermanagh, Northern Ireland, by the process of acid etching shows signs of predation or of having provided a habitat for organisms that required a hard surface upon or within which to live. The etched limestones were from a predominantly argillaceous series immediately underlying the widespread and prominent Dartry Limestone group. Within this fauna it is possible to distinguish damage indicating activity upon the living shells, and that reflecting settlement of organisms after death, in which only the shelly material was affected. It is assumed that any organism that lived wholly on the inner surfaces of valves, or which covered areas such as articulatory processes, or extended from the inner to the outer surfaces via the posterior margins must have colonized the valve after the death of the brachiopod.

Damage to living shells. One of the commonest signs of damage to brachiopod shells consists of neatly bored circular holes, usually penetrating the full thickness of the valve (Pl. 60, fig. 1). These holes vary from 0·1 mm. to just over 1 mm. in diameter and occur in as many as 50% of the collected pedicle valves of *Productina margaritacea*. However, the proportion is usually about 30% of pedicle valves and 15%, or less, of brachial valves, e.g. in *Rugosochonetes* cf. *celticus* about 35% of the pedicle valves and 7% of the brachial valves are bored. This higher occurrence of bored pedicle valves is probably a reflection of their accessibility to predators on or within the substratum, and of their immobility as compared to the free brachial valve. A surprising thing is that large valves may have three or four penetrating holes. It can only be assumed that the predators were only able to feed from the tissue close to the hole and bored in several places to expose more of the soft parts. The holes are commonly on the postero-median region of pedicle valves within about 6 or 7 mm. of the ventral beak, but not invariably so, and there seems to be no area in which they are particularly concentrated (text-fig. 1). Two borings out of forty-six into the pedicle valves of *P. margaritacea* were unsuccessful in that they do not penetrate the complete shell thickness. However, it is possible that these are the rare instances when predation was not successful in killing the brachiopod. This might have been possible if the boring took place just behind the shell edge and if the predator was unable to remove much of the internal mantle lobes. If this were so, the mantle could probably have repaired itself and subsequent deposition of secondary shell would have sealed the hole internally. From other evidence of damage to shells, it does seem that the

[Palaeontology, Vol. 9, Part 3, 1966 pp. 355–9, pl. 60.]

mantle was capable of repair allowing normal anterior growth to proceed and only leaving a temporary scar at the surface of the shell.

It is most probable that the predators involved were carnivorous gastropods living within the surface layer of the substratum. Modern gastropods, such as *Nucella*, bore similar holes, of about 1 mm. diameter, into lamellibranch shells. It is commonly noted that one valve of the lamellibranch is bored in preference to the other and this probably resulted from a preferred orientation of the shells, allowing greater accessibility to one valve. A comparable preference was shown by the Carboniferous predators for the pedicle valve of brachiopods. Fretter and Graham (1962) have pointed out that modern *Natica* only bores into shells when it is buried in sand. It is likely that the pedicle



TEXT-FIG. 1. Diagram of the pedicle valve exterior of *Productina margaritacea* (Phillips) showing the positions and approximate sizes of 44 borings through the valves.

valves of the Fermanagh brachiopods were partially buried in a soft substratum and that gastropods, occupying a similar niche to *Natica*, bored these areas of accessible shell. A boring of particular interest, seen on a German Permian strophalosiid, is one in which the boring did not penetrate the shell and which has a small boss within the circular cavity. *Natica* is known to bore upon its prey by rasping away the shell at the edges of the hole, so leaving a central boss similar to that seen on the Permian shell. Within the etched faunas there is a paucity of gastropod remains, and only a few specimens of *Platyceras*, *Euomphalus*, *Bellerophon*, and Subulitidae are to be found in residues from near Derrygonnelly, Co. Fermanagh.

Modern boring naticids and muricacids have been traced back to the Triassic and Cretaceous periods respectively, and no Palaeozoic genera are known to have been borers. However, it is likely that this style of feeding was employed by gastropods, and Fenton and Fenton (1931) have discussed such borings found in American Palaeozoic brachiopods. They distinguish borings with bevelled edges, such as described in Tertiary lamellibranchs by Hayasaka (1933), from those with parallel sides, as described here. Fenton and Fenton suggested that *Platyceras* may have been related to naticids, and therefore a borer, but this concept is no longer commonly accepted.

On the external surfaces of some shells are slightly twisting open canal-like borings. In some specimens these extend right through the shell substance, in others they appear as simple pits and holes. In some specimens of *Eomarginifera* these borings more or less follow the radial ribbing and measure between 0·8 and 1·5 mm. wide (Pl. 60, fig. 2). Their alignment with the ribs may result from the shell substance being thinner in these regions because of the supposed underlying mantle canals, which may have provided nutrients to the predator. There is no clear evidence as to whether these borings were made during the brachiopod's life or after its death. But as the borings invariably seem to enter the shell from its external surfaces, and tend to be concentrated around the ventral umbo, it is more likely that they were made while the shell was alive. Had the borings been made purely as a protective habitat it is probable that the thicker parts of the shell, between the ribs, would have been excavated. The borings are quite unlike the neat holes described above or the ramifications of bryozoans described below, and are thought to have been made by sponges.

Distortion of the normal shell growth is not uncommonly seen, either locally confined to a small area, or more extensive and with scar shell material dwindling anteriorly into normal growth. Sarycheva (1949) described forms of damage to productoid brachiopods and distinguished several morphological types based upon the extent and position of the damage. She suggested that much of the damage resulted from mechanical action, such as waves and moving stones, but that the jaw action of predators (p. 288) may have caused the more sharply localized damage. Sarycheva also described the irregular internal morphology, such as muscle scars, seen on some specimens. I believe that predation and irregular growth resulting from the close proximity of a foreign object account for most of the distorted shells seen in the Fermanagh fauna.

Irregularities in growth commonly developed from an indentation in the shell, as if locally crushed, or as a cleft extending to the valve margin. In the former instance the point of crushing may be confined to one valve or involve both valves, as can be seen in a specimen of *Delepinea destinezi* (Pl. 60, figs. 6, 7) from limestones of Lower Viséan age bordering Lough Erne. In this example a series of points have scarred and crushed part of the dorsal valve, producing a similarly shaped series of protuberances from the surface of the pedicle valve. The damage must have been considerable and broken right through the shell from the dorsal surface. Secondary shell occurs anterior to the damaged areas, so that the shell must have survived and continued its growth. In the scar area, and beyond, the costellation is irregular and remains distorted for a distance of about 20 mm. It seems likely that death would have resulted had this damage been inflicted to the visceral region, but that the mantle epithelium of the brachial cavity was capable of reformation and continued growth. Growth-lines radiate antero-medianly from the lateral edges of the scars, showing the way in which growth must have continued sealing around the front of the damaged areas, and indicating that the mantle edge was probably damaged. A crest was formed where these two growing edges reunited in front of the broken shell. Signs of the mantle edge having been damaged are to be seen in some specimens of *Krotovia spinulosa* and *Eomarginifera* in which a continuous groove developed up to the anterior margin (Pl. 60, fig. 5). Here shell substance was only deposited from the sides and normal growth was not resumed. One specimen of *Eomarginifera* (Pl. 60, fig. 4) appears to have had a portion of its pedicle valve removed without having irrevocably damaged the mantle. Here shell growth was continued level with the inner surface of the existing shell, but was not only secondary shell, as the external ornament was soon redeveloped and the shell levels became equal towards the anterior margin. It seems, therefore, that even after having had part of its shell ripped away, the mantle and mantle edge were still capable of shell deposition. The continuation or re-development of the normal surface ornamentation is indicative of normal primary shell formation, at the mantle edge, while featureless scar material was probably the product of the mantle surface along with the normal secondary shell substance.

So far as is known, the only possible predators large enough to inflict damage on the scale described above would have been fishes, probably members of the cladodont sharks. The deep impression left in the brachial valve of *Delepinea*, described above, matches the shape that is typical for a cladodont tooth. The impression lacks the mark of the large central cusp because of the deposition of secondary shell in that region, but the smaller marginal cusps have all left their marks. The teeth of these vertebrates are to be found occasionally in nearby sediments.

Damage to Dead Shells. One of the commonest forms of damage to shells is that of infestation, most likely by ctenostomatous bryozoans, belonging to the subphylum Ectoprocta. These stoloniferous, zooid-bearing organisms usually appear on the inner surfaces of the valves as thin crack-like tubes of about 0·04 mm. diameter. Older regions of the colony increase in size to about 0·1 mm. diameter and are covered by minute pores, but a gradation between the two sizes is rare. The stolons may be on the valve surface or more or less sunk into the shell. Rarely they disappear completely into the shell and may penetrate to the outer surface. Branching is common and the stolons may cross one another. Colonization of the valves commonly took place in a more or less radial fashion from one or more centres of growth, which became enlarged and commonly deeply sunk into the shell. The surfaces of the stolons of these older regions are closely covered by minute pores, giving a granular appearance, as if the zooids were crowded over the entire surface rather than being arranged in single rows, as along the thin newly formed stolons.

Of the described ctenostomatous genera (Bassler 1953), the nearest in morphology is *Vinella* Ulrich 1890, although the Fermanagh ramifications have more than a 'single row of small pores' (1953, G35) on many of the stolons. Further study of these organisms may reveal that they should not be referred to *Vinella* and that the pores themselves housed polypides rather than being the scars from where the zooecia have broken.

EXPLANATION OF PLATE 60

All specimens are silicified and collected from Co. Fermanagh.

Fig. 1. *Krotovia sp.*, showing six holes bored through the pedicle valve. BB52878, ×4·1.

Fig. 2. *Eomarginifera sp.*, showing borings on the visceral region of the pedicle valve. BB52893, ×4·1.

Fig. 3. *Plicatifera plicatilis* (J. de C. Sowerby), damaged shell showing irregularly developed plication. BB52924, ×3·8.

Fig. 4. *Eomarginifera sp.*, damaged and bored pedicle valve. BB52925, ×3·7.

Fig. 5. *Krotovia spinulosa* (J. Sowerby), damaged pedicle valve. BB52923, ×4·1.

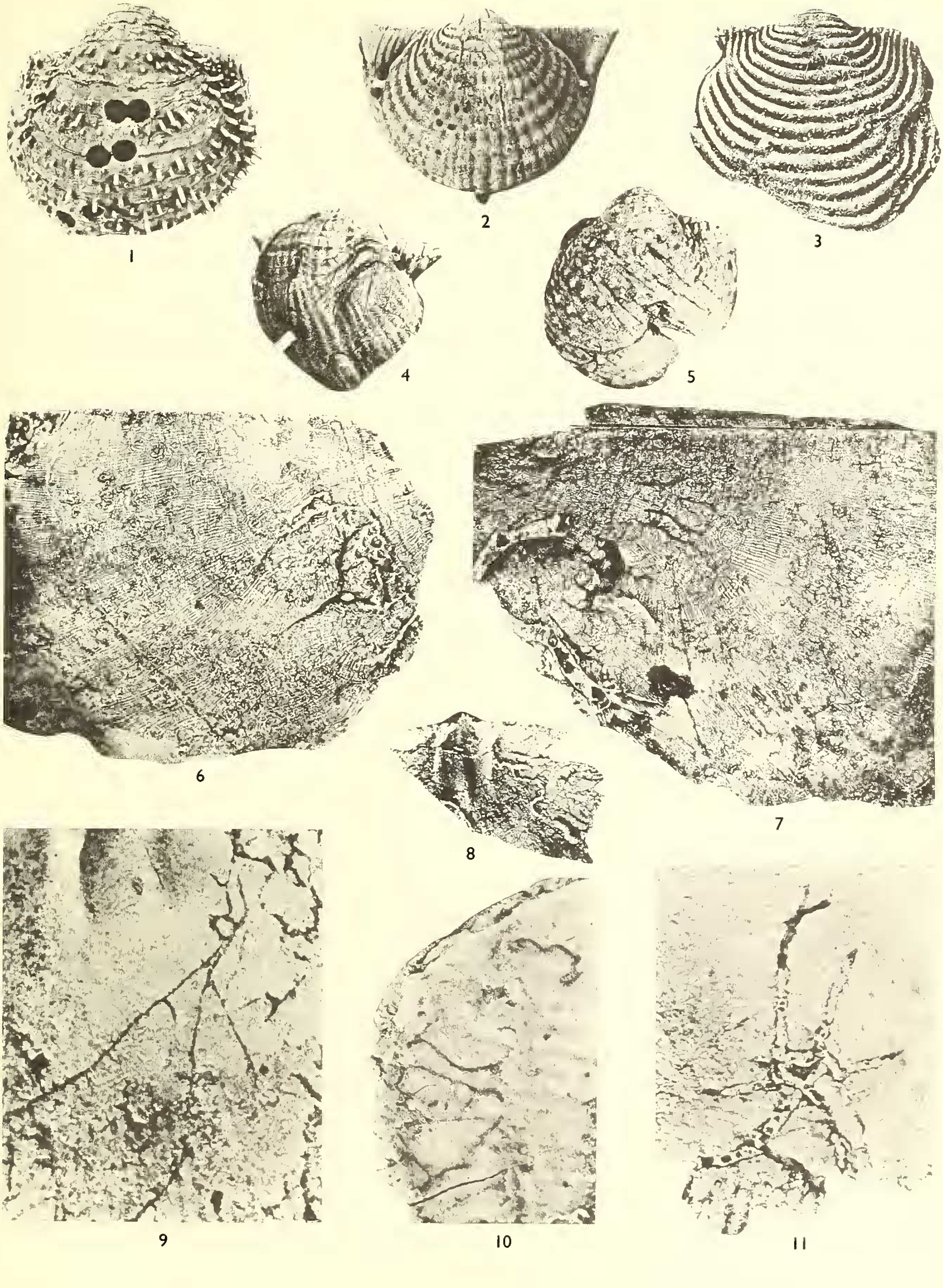
Figs. 6, 7. *Delepinea destinezi* (Vaughan), fragment of shell showing the damage believed to have been caused by a cladodont shark; viewed ventrally and dorsally. BB52927, ×1·2.

Fig. 8. *Schizophoria sp.*, fragment of pedicle valve showing worm tubes that developed over the dental plates. BB54634, ×4·1.

Fig. 9. Portion of the ventral interior of *Schizophoria* showing ctenostome infestation. BB52931, ×10·2.

Fig. 10. *Eomarginifera sp.*, portion of the upper, posteriorly directed, portion of the pedicle valve trail showing ctenostome infestation. BB52930, ×8·6.

Fig. 11. *Schizophoria sp.*, portion of the ventral interior showing a young ctenostome colony. BB52932, ×17.



BRUNTON, Predation and damage in Viséan brachiopods